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Published in:
Behavioral Ecology

DOI:
10.1093/beheco/arp146

Behavioral Ecology
doi:10.1093/beheco/arp146
Advance Access publication 5 November 2009

Predator escape tactics in birds: linking ecology and aerodynamics

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In most birds, flight is the most important means of escape from predators. Impaired flight abilities due to increased wing loading may increase vulnerability to predation. To compensate for an increase in wing loading, birds are able to independently decrease body mass (BM) or increase pectoral muscle mass (PMM). Comparing nearshore and farshore foraging shorebird species, we develop a theory as to which of these responses should be the most appropriate. We hypothesize that nearshore foragers should respond to increased predation by increasing their PMM in order to promote speed-based escape. Instead, farshore foragers should decrease BM in order to improve agility for maneuvering escape. Experiments on 2 shorebird species are consistent with these predictions, but on the basis of the theoretical framework for evaluating effect size and biological significance developed here, more experiments are clearly needed. *Key words:* aerodynamics, body mass, escape performance, flight, pectoral muscle, phenotypic flexibility, raptors, risk management. *[Behav Ecol 21:16–25 (2010)]*

Hunting and escape strategies of predators and prey are probably the result of a coevolutionary arms race (Dawkins 1999). Yet, this interaction is asymmetric. An individual prey has more to lose by failure to avoid a predator than predators by failing to catch a prey. Therefore, selection pressures to avoid being killed should be particularly strong for prey species.

Animals respond to approaching predators in many ways. They can startle the predator, stand their ground, crouch and stay put, or fly off (Caro 2005). For most birds, flight is the predominant escape mode. A reduction of speed or maneuverability is likely to increase the chance of being depredated once airborne (Howland 1974; Witter et al. 1994). Although it has become widely acknowledged that escape flight performance is influenced both by the muscle power available for fast forward flight and movements and by wing loading (i.e., the body mass [BM]/wing surface ratio) (Howland 1974; Hedenström and Alerstam 1992; Hedenström and Rosén 2001; Videler 2005), most experimental studies to date have investigated the effect of wing loading on flight performance without measuring possible compensation for flight capacity by changes in pectoral muscle size (Lima and Valone 1986; Witter et al. 1994; Gosler et al. 1995; Lima 1995; Kullberg et al. 1996, 2002; Lilliendahl 1997, 2000; Carrascal and Polo 1999; Burns and Ydenberg 2002; but see Lind 2001). However, there is evidence that compensation for flight capacity changes are possible: During migration, birds have been shown to adjust the size and capacity of specific body parts (Piersma and Drent 2003) including rapid reversible adjustments of pectoral muscle relative to BM levels (Lindström et al. 2002; Dietz and Piersma 2007). Furthermore, by experimentally inducing molt gaps, Lind and Jakobsson (2001) demonstrated that pectoral muscle size and BM can be independently regulated in response to wing loading. Such fine-tuning can additionally be influenced by predation danger (van den Hout et al. 2006).

When discussing body composition adjustments to predation danger, we must distinguish between, on the one hand, the mode of adjustment (adjustment in either overall BM or pectoral muscle mass [PMM], or a combination of both) and, on the other hand, the sensitivity to fuel load in terms of predation costs, that is, the extent to which a decrease in flight performance affects predation danger. Although a change in mass components may be advantageous in terms of flight performance, it will involve costs. For instance, a reduction in BM, though improving flight performance, also increases the risk of starvation (McNamara and Houston 1990; Witter and Cuthill 1993). Therefore, responses to predation threat are expected to reflect a trade-off between the benefits and costs of changes in BM components (Witter et al. 1995). The amount of energy stores that a bird is willing to sacrifice may depend on the predation costs that the corresponding extra BM would entail. Predation costs include the extent to which the negative impact of fuel load on flight performance affects survival probability. Lind (2004) argued that the importance of flight performance for predation danger increases as the distance from protective cover increases because small increases in wing loading have little effect on escape chances on such small distances. Generally, mass-dependent predation costs may be lower for species that can feed close to protective cover than for species that forage in areas devoid of protective cover (Dierschke 2003; Lank and Ydenberg 2003).

Birds living in open habitats, on mudflats for example, may be particularly sensitive to fuel load in terms of predation costs. For such habitats, vegetation and other topographical

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Received 7 April 2009; revised 10 September 2009; accepted 23 September 2009.

structures are not perceived as safe havens, but rather as obstructive cover, as these allow an undetected approach by predators (Piersma et al. 1993; Cresswell 1996). Vertical habitat structures will generally be avoided (Zwarts 1988; Rogers et al. 2006). However, due to their foraging specializations, some species are forced to forage close to the shoreline, where dunes, dikes, or vegetation obstruct their view of the horizon (Metcalfe 1984).

In this paper, we compare these nearshore and farshore foraging species. Using aerodynamic theory, we predict differences in their responses to predation in terms of BM and PMM. We also predict that species-specific morphological responses to predation are not only related to their escape tactic and related ecologies but may also be reflected in flight frame characteristics. Finally, we discuss molt, given that gaps in the wing affect wing loading and may influence the perception of predation danger (Lind 2001), and thus mediate phenotypic responses to predation threat. A brief description of how the predictions can be tested will be followed by a discussion of the results of such an experiment.

Escape scenarios: linking ecology and aerodynamics

The difference between nearshore and farshore escapers is best explained by considering 2 major generalizations based on the relative position of prey and predator, speed vectors between prey and predator when the prey detects the predator (Hedenström and Rosén 2001), and escape destination (Lima 1993).

Nearshore foragers

Shorebird species that tend to forage in the close vicinity of obstructive cover are often confronted with predators at close range as the physical properties of the habitat supply the predator with opportunities for undetected approach (Metcalfe 1984). Individuals aiming to reach a safe destination, such as water or salt marsh, require a speed-based accelerating escape (linear maneuverability) in order to reach that destination before the predator strikes. Such speed-based locomotion requires the ability of generating a high velocity of shortening in the locomotor muscles (Kumagai et al. 2000), whereas an increase of such speed-based escape abilities would call for a build up of fast-twitch muscle fibers (Rosser and George 1986). Such bird species are expected to respond to predation danger by PMM increase, which allows them to save on energy stores.

Measures for wing shape in this context include aspect ratio (wing span^2/wing area) (Warrick 1998; Hedenström and Rosén 2001) and wingtip pointedness/roundedness and convexity (Monkkonen 1995; Lockwood et al. 1998; Burns and Ydenberg 2002). The 2 measures are related: wing pointedness results in a high aspect ratio (Norberg 1989). Bird species employing speed-based escape are expected to have relatively low aspect wing ratios as the inertia of high aspect ratio wings (which increases with the square of their length) may compromise the mass-specific power output generated by wing flapping (Warrick 1998). Likewise, such bird species may have rounder wingtips, which are said to maximize thrust from flapping wings (Rayner 1993). Additionally, rounded wings produce relatively more lift toward the wingtip where the wing is moving faster but also more drag. These factors are likely to enhance flight performance at low speeds, particularly at takeoff from the ground and maneuverability by differential wing flapping (Swaddle and Lockwood 1998; Warrick et al. 1998).

Farshore foragers

The essential difference between the escape context of farshore and nearshore foragers is the distance between prey and predator at the time the prey detects the predator. Farshore foragers typically avoid foraging near obstructive cover (Rudebeck 1950–1951; Brown and Kotler 2007). This allows birds to detect an approaching predator from a relatively large distance, permitting relatively early take-off, and time to gain speed and prepare maneuvers. Gregariousness has additional advantages in this scenario as high levels of vigilance ("many eyes") combined with an unobstructed view of the horizon increases the chance of early detection (Krause and Ruxton 2002) and provides time to recruit flock members for a socially coordinated escape. Calidrid species (sandpipers) (Figure 1) are well-known for such united, erratic display flights to form flocks which appear to pulsate and maneuver as one organism (Rudebeck 1950–1951; Lima 1993), but time lags between detection and encounter with the predator allow even relatively solitary foragers to team up with such "escape units" (P.J.H., personal observation).

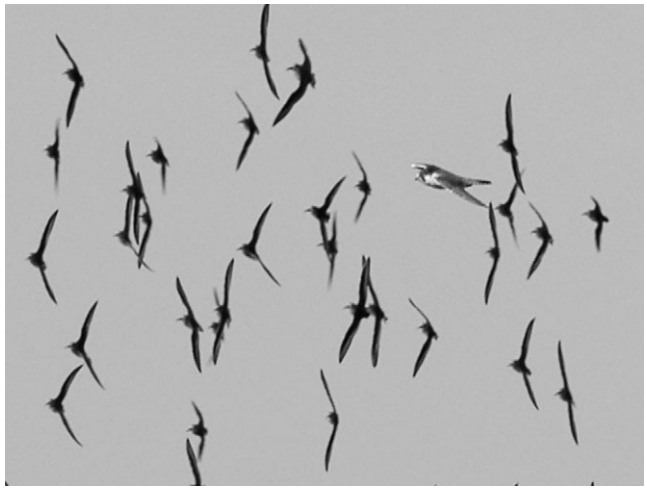

Figure 1
Photographic illustration of fast pure rotational banks by dunlins *Calidris alpina* chased by a peregrine falcon *Falco peregrinus*. Note that neither of the birds shows the flapping velocity asymmetries (see text). Instead, pronation/supination of the wing is apparent in most of the birds, particularly by the 2 closely paralleled birds in the lower middle of the picture. The photo, found on the World Wide Web, was taken by an anonymous photographer.

In such a scenario, turning maneuverability, rather than linear maneuverability, may be of paramount importance. Studies that focus on maneuverability commonly address low-speed maneuvering (Warrick and Dial 1998; Warrick et al. 1998), and less is known about flight maneuvers that are initiated at high speed. Warrick and Dial (1998) argue that at high speeds, birds can exploit the acquired lift forces to produce angle of attack asymmetries immediately, without preparation (i.e., an upstroke). High aspect ratio wings are most suitable for such maneuvers. "In addition," they write, "by not driving the wings through a downstroke while pronating/supinating, the bird directs most of the lift on the outside wing perpendicular to the roll axis and could theoretically produce negative angles of attack on the inside wing. The result would be a pure rotation bank, with the bird rolling around its center of mass at high angular accelerations." This would mean that, at higher speeds, birds can economize on muscle power for wing flapping, exploiting lift forces for turns. This is what the sandpipers in Figure 1 seem to do. At these high speeds, lift forces on the hand wing are the dominant forces as further from the center of gravity lever effects on the roll control will be stronger (Videler 2005). Now, inertia properties of the flight frame put limits on the turning radii, which the birds can perform

when escaping from a predator. This means that through a decrease in BM alone, birds can decrease turning radii. This can be mathematically demonstrated using aerodynamic theory as follows.

Steady flight in still air requires balanced forces where lift equals weight and thrust equals drag, as well as balanced moments of these forces about the center of gravity (Videler 2005). Warrick et al. (1998) describe that for a bird to change direction in a steady state turn (i.e., continuous lift production and nonflapping wings) it requires an initiating force asymmetry, followed by an arresting force asymmetry. Disparate forces produced by the wings cause the bird to roll into a bank (wings making an angle Φ to the horizontal), redirecting lift toward the desired direction of flight. Then, the initial force asymmetry must be reversed to halt the rolling momentum. Now, the bird turns at a constant rate, and no further force asymmetry is needed to maintain the bank once it has been established. We express the balanced forces in the vertical transversal plane acting on a bird that initiates a gambit by pronation/supination of the wings, thus engaging in a pure rotation bank and demonstrate that the turning capabilities are dominated by BM. We take equation 2 from Hedenström and Rosén (2001) as a starting point (Equation 1). This shows how to compute turning radius, r, of a bird circling with azimuthal velocity, v, from the radial forces acting on the bird. These are the inward directed component $L\sin\Phi$ of the lift force L which balances the outward directed centrifugal force Mv^2/r, where M denotes BM. This leads to

$$r = \frac{Mv^2}{L\sin\Phi}. \tag{1}$$

In the vertical direction, the force of gravity, Mg (g denoting the acceleration of gravity), is balanced by the upward directed component of the lift force:

$$Mg = L\cos\Phi. \tag{2}$$

Using the trigonometric relation $\cos^2\Phi + \sin^2\Phi = 1$, this yields

$$\frac{M^2g^2}{L^2} + \frac{M^2v^4}{L^2r^2} = 1, \tag{3}$$

Solving for the radius r yields:

$$r = v^2\left(L^2M^{-2} - g^2\right)^{-1/2} \tag{4}$$

Now, the lift force induced by flow around the wing is itself proportional to the squared velocity

$$L = \frac{1}{2}\rho v^2 S C_l, \tag{5}$$

where ρ = density of air at sea level = 1.23 kg/m^3, S = wing surface area, and C_l = lift coefficient = 0.5 (Hedenström and Rosén 2001). Defining proportionality constant α (kgm^{-1})

$$\alpha = \frac{\rho S C_l}{2}, \tag{6}$$

we have

$$L = \alpha v^2. \tag{7}$$

Inserting this into the expression for the radius, we find

$$r = \frac{v^2}{\left(\alpha^2v^4/M^2 - g^2\right)^{1/2}}. \tag{8}$$

Therefore, for large velocities,

$$\lim_{v\to\infty} r(v) = \lim_{v\to\infty} \frac{v^2}{\left(\alpha^2v^4/M^2 - g^2\right)^{1/2}} = \frac{M}{\alpha}, \tag{9}$$

the radius approaches its minimum, $r_{min} = M/\alpha$, which clearly decreases with decreasing BM M. We will illustrate these calculations when discussing our experiments.

Howland (1974) explains that at some high velocity an additional effect must set in, namely that of a limit to the centrifugal acceleration that a bird can withstand. Given that the animal is moving sufficiently fast that this limit is reached, then for every increase in velocity it must also increase its turning radius in proportion to the square of its velocity in order to stay within the limit of constant centrifugal acceleration (in general the lift of a wing will be proportional to the square of the velocity at which the bird moves). Above a certain level, speed will be lost at the expense of turning radius. This constraint can be counteracted by BM decrease.

In conclusion, we predict nearshore foragers to be generally speed-based escapers that respond to increased predation pressure by PMM increase. Farshore foragers are predicted to be agility-based escapers that respond to increased predation threat by a decrease in general BM.

Based on a comparative literature study among passerines, Swaddle and Lockwood (1998) concluded that species with relatively rounded wingtips and relatively short femora compared with tarsi were at a lower predation risk than species with more pointed wingtips and relatively longer femora. Burns and Ydenberg (2002) proposed that habitat-related escape tactics in 2 closely related Calidrid species may have contributed to differences in both wing and hind limb morphologies between the 2 species. Yet, they rightfully acknowledge that wing shape likely evolved under multiple, and possibly conflicting, selection pressures, related to predation, migration, reproduction (display flight), and foraging. For instance, it has been argued that the demands of migration may have set the stage for the high aspect ratio wings of many long-distance migrants, whereas special foraging techniques may have contributed to differences in wing shapes between coursing and hawking insectivorous bird species (Warrick 1998). Thus, differences in wing shape due to escape tactics may be subtle. We predict that speed-based escapers have relatively low aspect ratio, or relatively rounded wings, whereas socially coordinated escapers are predicted to have relatively high aspect ratio or relatively pointed wings. Finally, molt gaps decrease wing surface thus increasing wing loading. As this will decrease escape flight performance thereby increasing vulnerability to predation, compensatory measures are expected to be similarly associated to the birds' ecologies.

A first test of the predictions

Small flocks of birds may be randomly exposed to simulated predator attacks, for instance by gliding a raptor model overhead. BM (using a balance) and pectoral muscle thickness (PMT) (using ultrasonography) (Dietz et al. 1999a) may be measured before and after the experiment, limiting disturbance effects by the researcher as much as possible. To examine possible relationships between escape tactic and responses in pectoral muscle and BM, such experiments could be performed with different similar-sized species, with different ecologies (nearshore/farshore foragers). There are a number of shorebird species that typically forage in nearshore areas, such as rocky shores and sandy beaches (e.g., whimbrel *Numenius phaeopus*, black turnstone *Arenaria melanocephala*, ruddy turnstone *Arenaria interpres*, purple sandpiper *Calidris maritima*, sanderling *Calidris alba*, rock sandpiper *Calidris ptilocnemis*,

surfbird *Aphrizia virgata*, common sandpiper *Actitis hypoleucos*, spotted sandpiper *Actitis macularia*, and a number of *Charadrius* plovers). Others are more typical of open areas, such as red knot *Calidris canutus*, dunlin *Calidris alpina*, and western sandpiper *Calidris mauri*.

We performed such an experiment in the indoor Experimental Shorebird Facility at the Royal Netherlands Institute for Sea Research (NIOZ) with red knots (a farshore forager species) and compared this to a similar experiment (same facility, similar setup) with ruddy turnstones (a nearshore forager species) (van den Hout et al. 2006). We examined BM and PMT changes in response to exposure to a model predator. We only describe the methods of the red knot experiment, referring to van den Hout et al. (2006) for the turnstone experiment.

MATERIALS AND METHODS

Using mistnets, 50 red knots were caught on Richel (53°16′57″N, 05°23′82″E) and on Simonszand (53°29′28″N, 06°24′19″E), in the Wadden Sea, The Netherlands, on 8 August and 3 September 2005, respectively. We selected adults of the *islandica* subspecies (e.g., Nebel et al. 2000; Piersma 2007). The birds were housed in aviaries at the NIOZ in 4 flocks of 12 to 13 birds. The aviaries measured 3.85 m by 1.85 m and were 2.40-m high. Air temperature and photoperiod were determined by the ambient outdoor conditions. Each group of experimental birds was set free in the Mokbaai, Wadden Sea (53°00′37″N, 04°45′11″E) immediately after the experiments. From the beginning of their time in captivity, the birds were fed ad libitum with 2–4 mm mudsnails (*Hydrobia ulvae*), which had been collected from the Wadden Sea. Mudsnails were stored frozen and thawed immediately before use (Vézina et al. 2006).

Some of these birds were molting their primaries, and we were aware that this might confound our results. Therefore, to enable statistical control for molt later on, birds were scored for growth of primaries (0 = old, 1 = shed, 2 = quarter grown, 3 = half grown, 4 = 3 quarters grown, and 5 = fully grown feather—Ginn and Melville 1983). To estimate the size of the gap in the wing caused by missing or growing feathers, we used the measurement of wing raggedness, which corresponds to the molt score such that the sum of the molt score and the raggedness score is 5 for each new or growing feather. As neither an old nor a fully grown feather causes a gap, both have a raggedness score of zero (Bensch and Grahn 1993). Although this measure does not account for the position of the gap in the wing (Hedenström and Sunada 1999), it is nonetheless adequate for exploring possible molt effects within individuals.

The experiments took place from 21 August through 28 November 2005 in an indoor mudflat facility (7 × 7 × 3.5 m high; see figure in Mathot et al. 2009). During the experiments, a constant light:dark cycle was implemented (lights on from 0600 to 2100 h), with "moonlight" illumination being provided during the dark phase. We carried out 8 trials, each with a flock of 6 birds that were randomly selected from each of the 4 outdoor flocks. Each trial consisted of a 2-day habituation period, followed by a 5-day control and a 5-day experimental period. This time frame was used because it is expected to be sufficiently long to allow detectable changes in PMM and total BM (Dietz, Piersma, and Dekinga 1999; Piersma et al. 1999; van den Hout et al. 2006). The order of experimental and control periods was determined at random for each flock, with flocks receiving the experimental period first and last in 4 trials each.

During the trials 2 event types were used to simulate predation danger. The first consisted of a gliding sparrowhawk model accompanied by digital playback of wader alarm calls. This event lasted about 5 s. The stuffed model glided across one side of the indoor mudflat, passing over the food tray (see Mathot et al. 2009). The second event type involved presenting a model of a perched sparrowhawk supplied with a built-in electromotor which allowed head movement. The perched sparrowhawk was hidden behind a black curtain except during "perching" events, when the curtain was lifted and the perched model was rolled into the mudflat arena, for 1 min, approximately 0.5 m above the mudflat surface. During the experimental periods, "gliding" and "perching" events were carried out once each day at unpredictable times between 0930 and 1700 h with the constraint that events did not occur within 90 min of each other in order to allow sufficient time for focal observations between events. Behavioral responses to the raptor threats in this experiment, including details of observational methods, were discussed in a separate paper (Mathot et al. 2009).

In the previous experiment (van den Hout et al. 2006), it was established that shorebirds are able to distinguish predators from nonthreatening disturbances. Having shown this and trying to avoid any other disturbance of the red knots in the experimental arena, we did not provide a nonthreatening disturbance as control. During all phases of the trials (i.e., habituation, control, and experiment), at 1800 h the mudflat was briefly (10–30 min) flooded with seawater to help cleanse the sandy substrate. During this time, the birds could rest on an elevated roosting platform (Mathot et al. 2009). Food was also replaced at this time. Trays of freshly thawed mudsnails were provided in sufficient quantity to allow ad libitum feeding for the subsequent 24 h.

Morphological changes were measured as the differences between the onset and the end of each control and treatment period. BM was measured to the nearest 0.1 g on a balance (Sartorius, type 3862). Pectoral muscle size (pectoral muscle thickness [PMT], to the nearest 0.1 mm) was measured by P.J.H. and in the last 2 trials by Anne Dekinga, using an ultrasound apparatus with a 7.5-MHz linear probe (Pie 200, Pie Medical Benelux BV, Maastricht, The Netherlands; for further details, see Dietz, Dekinga, et al. 1999. As P.J.H. was aware of the treatment that birds were exposed to, in each session of ultrasound measurements, 3 dummy birds were randomly included to test for observer bias. There was no such observer bias as treatment and control values did not differ for these dummy birds (general linear models, $F_{1,24} = 0.139$, $P = 0.713$). The measurements were otherwise "blind" in the sense that no readings were made by the observer but only ultrasound pictures that were subsequently interpreted by a second observer. Ultrasound measurements showed a repeatability of 0.83 for P.J.H. and 0.80 for Anne Dekinga (Lessells and Boag 1987; Dietz, Dekinga, et al. 1999). We computed PMM (g) from PMT (mm) using the predictive equations derived from a calibration exercise on red knot carcasses (these birds died as a result of catching accidents on the Banc d'Arguin, except for 3 birds that collided with a light house in the German Wadden Sea): for the measurements taken by P.J.H.: PMM = –0.35 + 0.40 PMT ($R^2 = 0.24$, $N = 16$, $P = 0.030$); for Anne Dekinga : PMM = –9.58 + 0.28 PMT ($R^2 = 0.40$, $N = 18$, $P = 0.003$). During the first experiment (which started off with a control treatment), no pectoral muscle data were obtained because of instrument failure. This limited the comparisons involving PMT to 7 trials.

Data were analyzed using linear mixed effects (LMEs) models from the package "nlme" in R (v. 2.6.1). LMEs provide estimates of the influence of fixed effects on the mean and random effects on the variance, accounting for the nonindependence of errors resulting from the repeated measures on individuals. Statistically, trials are comprised of the successive

treatments each carried out with a different "group." Using repeated measures, each individual served as its own control. To remove body size related variation among individual birds, all mass variables were standardized by dividing them by the values at the start of the trial. We tested for differences in BM and PMT between the predator treatment and the control, using models with treatment, treatment order (control or predator first), the interaction of treatment and treatment order as fixed effects, and individual within group within order as a random effect. As treatment order could not be tested as both a fixed factor and as part of a nested complex of random factors (treatment order/group/individual), we compounded order and group into unique combinations, leaving only 2 nesting levels (~1|treatment order&group/individual).

Although alternating "treatment order" would serve to control for seasonal effects, including molt, we chose to include raggedness of the wing as a covariate in the analysis (in the LME package of R, the covariate, raggedness, is used in the model statement, thus considered a fixed effect) to control for possible effects of molt on the response variables of interest (BM and PMT). Midpoint measurements of primary molt would create too much disturbance to the experimental birds, and consequently, we took molt scores immediately after each experiment. However, as during the first 3 trials primary molt data were taken immediately before the experiment, we interpolated these values to values expected at the end of a trial, by calculating the speed of growth for each primary. These calculations were based on primary molt patterns estimated from weekly measures of 55 red knots kept in the outdoor aviaries at our institute in autumn 2001 and 2002.

Assumptions of normality and homoscedasticity were verified by visual inspection of probability plots. Raggedness values were square root + 0.5 transformed to meet requirements of normality (Zar 1999). We ranked all possible models using the Akaike Information Criterion (AIC) (Akaike 1974), and selected the highest ranked model (with lowest AIC) as our final model.

Table 1
Model selection for tests of responses of BM and PMT to raptor exposure

Model (random = ~1|order&group/individual) dependent variable	BM		PMT	
	Rank	AIC	Rank	AIC
Treat + order + rag + treat × order + treat × rag + order × rag + treat × order × rag	8	−289	8	−196
Treat + order + rag + treat × order + treat × rag + order × rag	7	−295	7	−202
Treat + order + rag + treat × order + treat × rag	6	−303	6	−209
Treat + order + rag + treat × order + order × rag	5	−305	5	−209
Treat + order + rag + treat × rag	4	−313	4	−217
Treat + order + rag + treat × order	3	−314	3	−217
Treat + order + rag	2	−323	2	−225
Treat + rag	1	−330	1	−232

Treat, treatment; order, treatment order; rag, raggedness. In the LME package of R, the covariate raggedness is used as a fixed factor. The minimal model, with lowest AIC value, was chosen for both dependent variables.

EXPERIMENTAL RESULTS

On the appearance of both the gliding and the perching sparrowhawk, red knots always took flight and remained airborne for 34.7 ± 1.3 s (mean ± standard error of the mean [SEM], $N = 240$) after hawk flight events and 28.2 ± 1.3 s (mean ± [SEM], $N = 240$) after hawk perching events.

The minimally adequate model for changes in both BM and PMM included treatment and raggedness as fixed effects (Table 1). Exposure to the raptor models resulted in average BM reduction of 2.6% ($P < 0.001$; Table 2). When the control preceded the predator treatment, BM increased with an average 4.8% (from 122.1 to 128.0 g) during the 5-day control phase of the experiment and decreased by 2.3% (from 128.0 to 125.1 g) during the subsequent 5-day predator phase. In contrast, when the raptor models were presented first, despite a tendency for BM increase during the entire experimental period (see values with respect to baseline in Figure 2A), BM at the end of the raptor treatment was not different from starting mass, but subsequently increased during the control phase by 2.7% (from 126.7 to 130.0 g; Figure 2A). Unlike BM, pectoral muscle size was not affected by the raptor model intrusions ($P = 0.562$; Table 2; Figure 2B).

In the model testing for the effects of treatment on BM, the random factor "group," compounded with "order" (see MATERIALS AND METHODS) was responsible for 56% of the random error. This was around 23% for "individual" nested within "group&order" (Table 3). In the model addressing pectoral muscle as the response variable, these values were 33% and 49%, respectively (Table 3). Molt (measured in raggedness values) tended to affect BM ($P = 0.090$; Table 2), but this effect was not significant; neither was the interaction term treatment × raggedness ($P = 0.950$). Raggedness, however, did influence PMT ($P < 0.001$; Table 2). Yet, neither treatment ($P = 0.562$; Table 2) nor the interaction term treatment × raggedness significantly affected PMT ($P = 0.318$). Analysis of the interaction terms indicate that differences at individual or group level in primary molt phase did not confound the effects of predator exposure on either BM or PMT.

Table 2
LME test results for effects on values of BM and PMT

Fixed effects	Effect size	Confidence interval	Degrees of freedom	*t*	*P*
Dependent variable: BM					
Treatment	−0.026	−0.036 to-0.015	1	−4.962	<0.001
Raggedness	−0.010	−0.022 to 0.002	1	−1.735	0.090
Dependent variable: PMT					
Treatment	−0.005	−0.023 to 0.013	1	−0.585	0.562
Raggedness	0.039	0.021 to 0.058	1	4.256	<0.001

The results for PMT were based on trials 2–8 only, due to instrument failure during the first trial.

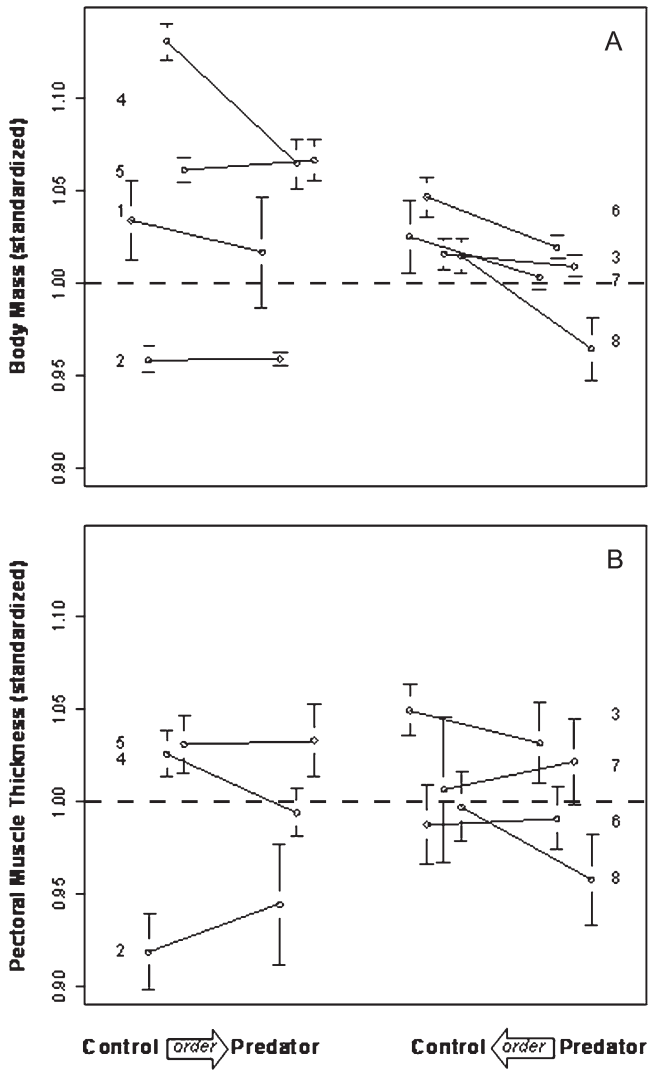

Figure 2
Changes in BM (panel A) and PMT (panel B) due to simulated raptor attacks compared with control treatment for each of the experimental trials separately. Variance around the means is shown by error bars (±1 standard error). The values are averages of 6 birds and were standardized to the values at the start of the trial (dashed lines denote baselines). Treatment orders (predator or control first) are depicted explicitly. Trial 1 for pectoral muscle is missing due to instrument failure.

Table 3
Random effects

Random effects Dependent variable: BM	Standard deviation	Relative contribution to variance (%)
Group&order	0.0398	55.9
Group&order/individual (intercept)	0.0247	21.5
Group&order/individual (residual)	0.0254	22.7
Dependent variable: pectoral muscle size		
Group&order	0.0334	32.6
Group&order/individual (intercept)	0.0411	17.9
Group&order/individual (residual)	0.0248	49.4

Note that group and order were compounded to one random factor (see MATERIALS AND METHODS). Note that R (nlme package for mixed models) treats the covariate raggedness as a fixed effect.

DISCUSSION

We used aerodynamic theory to develop predictions for the morphological response to predation danger of different classes of bird species, based on differences in their ecologies. Escape speed should be critical for nearshore species owing to the short predator detection distances, which should favor higher PMM. In contrast, farshore species should favor maneuverability and decrease mass in response to predation danger. A comparison of the red knot experiments with an earlier experiment with ruddy turnstones (van den Hout et al. 2006) provide preliminary evidence for species-specific morphological responses to predation which match the differential ecologies of those species.

After 5 days of exposure to simulated predator events, red knots decreased their overall BM, whereas PMM remained unchanged. Ruddy turnstones showed a different morphological response than red knots, increasing PMM without a significant increase in BM (fat-free mass did not change either). Instant responses to predator exposure also differed between these species: whereas red knots as a rule immediately flew off, ruddy turnstones generally responded by crouching and freezing.

The differences between red knots and ruddy turnstones in morphological response to predation are consistent with the predictions outlined earlier based on differences in their ecologies and related escape tactics. Ruddy turnstones feed in shoreline habitats, mainly foraging in small and scattered groups (Metcalfe 1986). They occur on beach-cast wrack and near the cover provided by rocks and other habitat structures (Cramp et al. 1983; Metcalfe 1984; Fuller 2003). Here, they are particularly vulnerable to surprise attacks by raptors such as sparrowhawks *Accipiter nisus* L. and large falcons, *Falco* species (Metcalfe 1984; van den Hout et al. 2008). When attacked by a raptor, ruddy turnstones have the option to freeze in the cryptic environment of crevices. However, if capture is imminent (Ydenberg and Dill 1986), they rely on a speed-based escape, often toward an open water surface (Whitfield et al. 1988) or into saltmarsh vegetation (Lima 1993). In view of the close range at which these species generally detect the predator, the early stage of escape is decisive for survival. This requires fast take-off and acceleration, that is, a speed-based escape. Increasing power output by boosting pectoral muscle best matches such an escape scenario.

In contrast, red knots tend to forage in large flocks in very open mudflat habitats avoiding topographical structures that would allow raptors to attack by surprise (Piersma et al. 1993; van den Hout et al. 2008). Other than ruddy turnstones which are often ambushed by raptors, through the "many eyes" available for scanning an unobstructed environment, red knots, as a rule, have more time to prepare themselves for an escape response. As soon as an aerial attacker is detected, red knots take flight as a flock and perform coordinated aerial escape flight maneuvers (Lima 1993; van den Hout et al. 2008). As predicted, rather than responding to predation danger by increasing the size of their pectoral muscles as in ruddy turnstones (van den Hout et al. 2006), red knots responded with a decrease in BM (though not at the expense of PMM) in favor of turning maneuverability. Applying the earlier mathematical calculations, we visualized the results of the red knot experiments in Figure 3. This figure shows that the benefit for red knots is 2-fold. First, the BM reduction directly reduces inertia and thus turning radius (Origin to position A); second, by decreasing BM, whereas

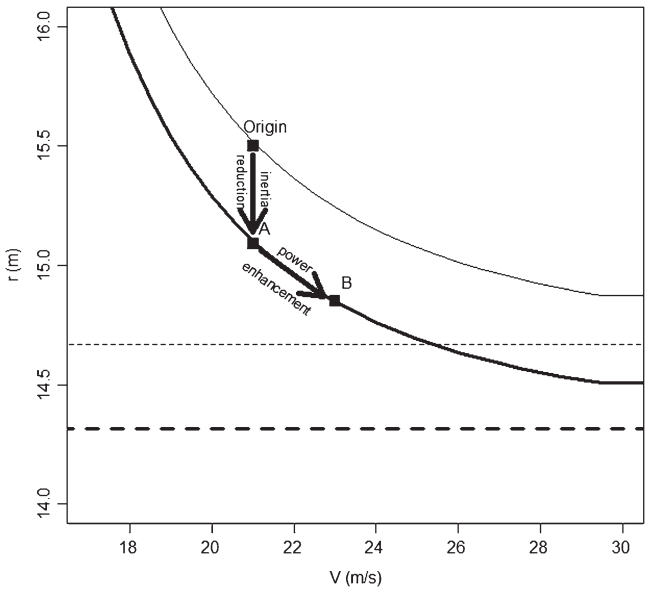

Figure 3
Isoclines reflecting turning radii as a function of velocity, as predicted by the model of Hedenström and Rosèn (2001), shown for the average of both orders (raptor control and vice versa) in the experiment. This returns 129.0 g for control (thin curve) and 125.9 g for the predator treatment (thick curve). Predicted minimum turning radii for birds in the raptor treatment and the control are determined by the asymptotes in the figure, yielding 14.67 m (thin dashed line) and 14.32 m (thick dashed line), respectively. Calculations of the asymptotic values were given earlier in the text. The 2-fold benefit of a decrease in BM is shown qualitatively: Origin to position A denotes the decrease in turning radius due to decreased BM; A to B shows the additional decrease in turning radius due to a relative increase in power output (see text). The ruddy turnstones in van den Hout et al. (2006) would move along a turnstone-specific isocline, toward higher speed, with a minor decrease in turning radius (equivalent to the trajectory from A to B in this figure).

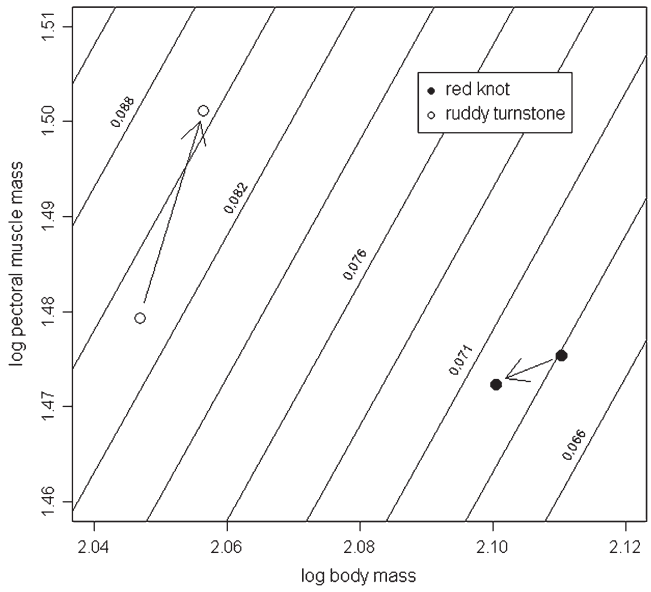

Figure 4
Phase space with lines for equal flight capacity ($PMM/BM^{1.25}$) (Dietz et al. 2007), for ruddy turnstones (van den Hout et al. 2006) and red knots (this study), showing that in response to raptor model intrusions both species increase flight capacity, red knots by decreasing BM and ruddy turnstones by increasing pectoral muscle size (all data were log transformed). Vector directions are based on average values. Small changes in BM (for ruddy turnstone) and pectoral muscle size (for red knot), although insignificant, contribute to the vector directions.

keeping pectoral muscle size unchanged, red knots increase power output and thus velocity, which leads to a further reduction in the turning radius (from A to B). Instead, the ruddy turnstones increase PMM (van den Hout et al. 2006), moving them away from the *y* axis along a turnstone-specific isocline, which mainly results in higher speed.

The benefit of BM decrease for overall flight capacity can also be demonstrated using the aerodynamic considerations for flight performance (based on wind tunnel studies) in Dietz et al. (2007). They predicted that for flight performance to remain constant, PMM should scale allometrically with BM to the power 1.25. In our experiment, in the control phase, red knots obtained an average BM of 129.0 g and a PMM of 29.9 g. The birds that decreased BM to 126.0 g after the raptor scares obtained a pectoral muscle of 29.7 g, 2.4% higher than the 29.0 g that would follow from this allometric relationship. Thus, red knots, after exposure to predators, as well as gaining greater maneuverability during the predator phase of the experiment, also achieved increased flight capacity ($PMM/BM^{1.25}$; Figure 4).

Our experiment was not designed to examine the effects of primary molt (raggedness) on mass components. Instead, we were confronted with some molting birds as a result of logistical (seasonal) constraints. Still, the examination of molt as a covariate yielded an interesting insight. There are no many studies on the effect of primary molt on pectoral muscle and most address waterfowl with respect to their virtually flightless period (Piersma 1988; Fox and Kahlert 2005, but see Lind and Jakobsson 2001). We now see that molt correlates with a significantly larger pectoral muscle size in a shorebird fully capable of flight. However, in our experiment the correlation between molt and pectoral muscle size was independent of the effects of predation threat on BM. Furthermore, there is no evidence that the absence of effect on pectoral muscle size is due to molt effects (Table 1).

As predicted, the difference in escape behavior of red knots and ruddy turnstones is not only correlated with their different ecologies but is also associated with differences in wing morphology. Although both red knots and ruddy turnstones are long-distance migrants with the predicted long slender wings (Alerstam and Lindström 1990; Marchetti et al. 1995), the aspect ratio of ruddy turnstone wings is 10% lower (7.9 ± 0.11, $N = 29$) than of red knot wings (8.7 ± 0.05, $N = 65$; $t = -5.85$, degrees of freedom $= 39.6$, $P < 0.001$), indicating that ruddy turnstones have relatively shorter and broader wings than red knots.

For red knots, maintaining coordinated movements with the rest of the flock is critical for any given individual in order to avoid being singled out in a one-to-one chase with the raptor (Caro 2005). This means that even subtle differences in maneuverability performance would translate into large differences in the probability of being killed. In view of the risks of being less agile than other flock mates, we expect selection for prey to have the ability to monitor the state of conspecifics in the same and different groups so that they assess relative vulnerability and respond appropriately (Cresswell and Quinn 2004). In such a game-theoretic scenario, for birds facing a trade-off between safety and energy even a subtle sacrifice in energy stores could thus have a significant payoff in terms of survival. However, the present experiment does not tell us whether in nature a period of more than 5 days of elevated danger would yield larger effects than we detected.

Previous observations have shown that PMM rapidly tracks changes in BM in red knots (Lindström et al. 2000). Thus, if the morphological changes observed in red knots following exposure to predators were merely a passive consequence of the increased flying and reduced feeding rates following exposure to predators, we would expect the PMM to decrease. Similarly, it seems unlikely that, in the red knots, flight activity due to the raptor disturbance caused pectoralis hypertrophy and simultaneous mass loss. Swaddle and Biewener (2000) showed that, as opposed to the muscle use–disuse hypertrophy–atrophy hypothesis (Marsh 1984; Gaunt et al. 1990), PMM in starlings induced to perform more take-off flights actually decreased as a result of exercise. In contrast, the red knots in our experiment, whereas decreasing BM, apparently defended PMM, thus increasing their flight output, likely as an antipredation measure rather than responding to workload (see also Witter et al. 1994). Similarly, in the experiment on ruddy turnstones (van den Hout et al. 2006), if changes in mass of body components were simply a consequence of behavioral changes induced by exposure to predators, changes in lean mass and PMM should have been correlated with one another. Instead, in ruddy turnstones the increase of PMM was decoupled from lean mass. We suggest that the turnstones' reluctance to fly on raptor intrusions (van den Hout et al. 2006), which in nature would be enabled by their cryptic environment, additionally serves to conserve muscle power in the case that escape becomes inevitable. The fact that ruddy turnstones, though not flying, increased pectoral muscle size, whereas red knots, while engaging in escape flights, did not (at least not in absolute sense) also hints to controls other than "use–disuse" mechanisms of these body components (Dietz, Piersma, and Dekinga 1999; Portugal et al. 2009).

Flock was included as a random effect in our model because it was not a variable of interest for the hypothesis we were testing. However, our data clearly show strong differences between groups in their morphological response to predation. Although we could develop hypotheses for why groups differed (e.g., differences in group composition such as sex, dominance, or personality profiles), this was not the focus of the current study. Despite large variation between groups, we still detect a significant effect of treatment on changes in BM, which suggests that treatment (predator/control) is an important factor mediating changes in BM.

The fact that several experimental studies (as reviewed in Caro 2005) report higher threshold values for BM to impair flight velocity or angle than the 2.6% BM change reported in this study (Table 1), does not refute our conclusions for at least 2 reasons. First, rather than BM, or even wing loading, alone, the ratio of pectoral muscle to BM reflects flight capacity (Lindström et al. 2000; Dietz et al. 2007). The impaired flight performance in the experiments testing flight performance as a function of wing loading may well have been caused by minor changes in this ratio, instead of BM increase alone. In fact, compensatory PMM increase may explain why other studies failed to find an effect of a moderate BM increase (Kullberg et al. 1998; van der Veen and Lindström 2000), even though effects were evident with high fuel loads (Kullberg et al. 1996; Dietz et al. 2007). Second, most studies measured only one or few maneuvers, which may come close to the natural situation of a passerine escaping into nearby cover. Yet, this does not compare to the persistent maneuvering of shorebirds escaping in a flock (Rudebeck 1950–1951; Lima 1993). In fact, just as human athletes experience in acrobatics (Fox et al. 2008), for example, in a balance beam routine, in birds minor agility "deficiencies" may add up to a fatal error in a sequence of maneuvers.

Proposing a research portfolio

This study provides preliminary support for the hypotheses developed in the introduction. However, further studies are required. Although use of ultrasound equipment for measuring pectoral muscles may be logistically unfeasible for many researchers, dental alginate exists as a cost effect alternative for obtaining coarse estimates of pectoral muscle size (Selman and Houston 1996).

To test whether changes in body composition as detected in experiments are biologically meaningful, additional experiments may be needed, in which flight performance parameters, such as linear acceleration, and turning speed and radius are coupled to differences in BM and PMM, respectively. Specific methods may depend on the size of the experimental bird species. To our knowledge, in all flight performance studies, birds of which flight performance was tested accelerated from a stationary position (Swaddle et al. 1999; Lind 2001; Burns and Ydenberg 2002), thus basically addressing a speed-based escape mode. Likewise, detailed studies of maneuverability typically involve maneuvering at relatively low speed (Warrick 1998, Warrick et al. 1998). To our knowledge, high-velocity maneuvers have never been studied in detail due to logistical constraints. Even more logistically challenging, but necessary for a full understanding of the proposed relationship between escape tactic and adaptive changes in body composition due to raptor threat, would be to measure flight parameters of birds involved in socially coordinated escape flight (for inspiration, see Potts 1984).

Other tractable systems, in addition to nearshore and farshore shorebird foragers, for testing this hypothesis include passerine taxa. The Emberizinae are a subfamily of the Passeriformes, which are notable for a high diversity of escape tactics (Lima 1993). For instance, within Fringillidae, a diversity of escape tactic from herbaceous- and woody-vegetation-dependent escape tactics is represented (Lindström 1989). Several arboreal, socially feeding fringillids (crossbills *Loxia species*, pine siskins *Carduelis pinus*, evening grosbeaks *Coccothraustes vespertinus*) employ highly coordinated flight and flushing behavior. This may be related to the use of more exposed feeding habitat due to weak familiarity with the location and nature of protective cover of these nomadic species (Lima 1993). We hope that this study will initiate a portfolio of novel studies in phenotypic flexibility and predation in the context of a species' ecology.

FUNDING

Natural Sciences and Engineering Research Council discovery grant to Luc-Alain Giraldeau (to K.J.M.)

We are very grateful to Maarten Brugge and the crew of the research vessel *Navicula* for help with the catching of the experimental red knots and for fishing mudsnails, to Anne Dekinga for performing ultrasound measures in the last 2 experimental trials, to François Vézina for assistance in the lab, to Jan van Gils for discussion and suggesting the isocline approach, and several anonymous referees, particularly Will Cresswell, for feedback. We thank Jeroen Reneerkens and Maurine W. Dietz for valuable comments on a draft, and Tamar Lok for statistical advice. The experiments complied with Dutch law regarding animal experiments (DEC[DierExperimentenCommissie]-licence NIOZ 04.04).

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